FORESTRY

ERDA REPORT 100

Nutrient Deficiency Symptoms in Container-grown Douglas-fir and White Spruce Seedlings

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90-03813/

Nutrient Deficiency Symptoms in Container-grown Douglas-fir and White Spruce Seedlings

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December 1989

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BC

Funding for this publication was provided by the Canada-British Columbia Forest Resource Development Agreement - a five year (1985-90) $300 million program cost-shared equally by the federal and provincial governments.

Canadian Cataloguing in Publication Data

Van den Driessche, R., 1933-
Nutrient deficiency symptoms in container-grown Douglas-fir and white spruce seedlings

(FRDA report, ISSN 0835-0752 ; 100)

Issued under Canada-BC Forest Resource Development Agreement.
Co-published by B.C. Ministry of Forests.
"Canada/BC Economic & Regional Development Agreement."
Includes bibliographical references.
ISBN 0-7726-1057-6

1. Douglas fir - British Columbia - Nutrition. 2. White spruce - British Columbia - Nutrition. 3. Douglas fir - British Columbia - Seedlings, Container - Evaluation. 4. White spruce - British Columbia - Seedlings, Container - Evaluation. I. Canada. Forestry Canada. II. British Columbia. Ministry of Forests. III. Canada-British Columbia Forest Resource Development Agreement. IV. Canada/BC Economic & Regional Development Agreement. V. Title. VI. Series.

SD397.C7V36 1990 634.9'752 C90-092029-7

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This is a joint publication of Forestry Canada and the British Columbia Ministry of Forests.

Produced and distributed by the Ministry of Forests, Research Branch.

For additional copies and/or further information about the Canada-British Columbia Forest Resource Development Agreement, contact:

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ABSTRACT

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and white spruce (*Picea glauca* (Moench) Voss) were grown in a container nursery at different levels of macro- and micronutrients to produce deficiency symptoms. In 1987, seedlings were grown in 3-13 styroblocks (PSB 313) using peat and perlite rooting medium, and each of the macronutrients was applied at four levels including 0. High levels were N = 200, P = 50, K = 100, Mg = 50, and S = 75 mg L^{-1} of nutrient solution. Different levels of Ca were obtained by adding $CaCO_3$ to the rooting medium. In 1988, seedlings were grown in perlite contained in Leech cells, and deionized water was used for preparing nutrient solutions and for watering. Four levels of the micronutrients Cu, Zn, Mn, Mo, B, and Fe were tested, with the fourth level about 10 times the usually recommended to look for toxicity symptoms.

Deficiency symptoms for all 12 elements except Ca, Mg, and Mo developed, as well as toxicity symptoms for Fe and Cu. Symptoms were photographed and seedlings were sampled in the middle of the growing season (June or July) and in October for measurement of height, dry weight, and nutrient concentration in tissue. Nutrient deficiency symptoms are summarized, and nutrient concentrations expected in each species after 12 weeks growth are presented. During the first year of growth, nutrient concentrations in actively growing seedlings appear to be substantially higher than concentrations regarded as adequate in dormant needles of older trees.

ACKNOWLEDGEMENTS

Technical assistance was provided by D. Ponsford, R. Planden, and J. Ogg. Photographs of macronutrient symptoms were taken in October 1987 by J. Thomson. Chemical analysis was conducted under the direction of M. Vallance and C. Dawson, and guidance in statistical analysis and computing was obtained from W. Bergerud.

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INTRODUCTION

In container nurseries using a peat-based growing medium all nutrients must be supplied except perhaps for Ca and Mg. Nutrients are usually supplied as soluble salts in solution, and concentration of nutrients and frequency of application of the solution have a major effect on the quality of the stock produced. The composition of mineral nutrient solutions suitable for growing conifer seedlings is well known (Fowells and Krauss 1959; Ingestad 1962; van den Driessche 1976, 1978; Tinus and McDonald 1979). However, several factors, including difficulties in manufacturing completely soluble fertilizers to supply all nutrients, differences in peat, and pH and salt content of water supply, can result in the development of nutrient imbalances, which are most commonly manifest as deficiencies. Nutrient deficiencies that result in reduced growth should prompt the nursery grower to obtain a seedling chemical analysis. Sometimes, though, the deficiency is not recognized until symptoms appear. In this case, diagnosis on the basis of symptoms can be attempted, but it should always be corroborated with chemical analysis.

Descriptions of nutrient deficiency symptoms in conifers have been summarized by Morrison (1974) and Ballard and Carter (1986), and colour plates showing deficiency symptoms have been published (Baule and Fricker 1970; Will 1987)[1]. These generally illustrate trees rather than seedlings, so the present work was carried out in an attempt to illustrate deficiency symptoms in seedlings of two important species, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and white spruce (*Picea glauca* (Moench) Voss), grown in British Columbia container nurseries. The purpose of the experiments was to develop deficiency symptoms in container seedlings under conditions similar to those in operational nurseries, and to obtain photographs and chemical analyses. A further objective was to see whether high levels of micronutrients could cause toxicity symptoms and reduce growth.

METHODS

Design

In both macro- and micronutrient experiments, six nutrients were each applied at four levels to Douglas-fir and white spruce seedlings. Nutrients and levels were fully randomized in two blocks per species. The treatment cell consisted of a 3-13 styroblock (198 55-mL cavities) in the macronutrient experiment, and a Leech cell block (96 130-mL cavities) in the micronutrient experiment. In each year a complete experiment occupied 96 container blocks.

Nutrient Solutions

Two litres of nutrient solution were applied to each styroblock twice a week after germination was complete. Application was with a watering can, and a screen was placed around the styroblock or styroblocks were moved out of the experiment so that adjacent styroblocks received no solution. In the macronutrient experiment, nutrients were supplied at relative levels of 0, 1, 2.5, and 10 within a treatment series (Table 1). All other macronutrients were supplied at level 10 within that series. Micronutrients were added to all solutions at the same level (Table 2). Analysis of mains water, used for preparing solutions and irrigation, showed concentrations of 0.28 mg K L^{-1}, 9.9 mg Ca L^{-1}, and 0.86 mg Mg L^{-1}. Analysis for other nutrients was not conducted.

In the micronutrient experiment, micronutrients were supplied at relative levels of 0, 1, 10, and 100 within a treatment series (Table 3). All other micronutrients were supplied at level 10 within the series (i.e., at the second highest level). Boric acid and iron chelate solutions were prepared and applied separately. Macronutrient solutions had closely similar concentrations to level 10 of the macronutrient experiment, and a Ca solution was added because no Ca was added to the medium (Table 4). The Ca solution was applied to the containers separately to avoid precipitation of other nutrients in solution. Deionized water was used for preparing nutrient solutions and all irrigation. Analysis of this water for all nutrients showed measurable amounts of N (2 mg L^{-1}), S (0.9 mg L^{-1}), Ca (0.05 mg L^{-1}), and Zn (0.04 mg L^{-1}).

---

[1] An interesting group of projection slides was recently issued by Kali und Salz AG, Postfach 102029, D-3500 Kassel, West Germany, showing symptoms of K and Mg deficiency in *Pinus sylvestris* and *Picea abies*.

TABLE 1. Macronutrient treatment concentrations (mg L^{-1})

Nutrient	Source	Level			
		0	1.0	2.5	10
N	NH_4NO_3	0	20	50	200
P	H_3PO_4	0	5	12.5	50
K	KCl	0	10	25	100
Mg	$MgCl_2 \cdot 6H_2O$	0	5	12.5	50
S	Na_2SO_4	0	7.5	18.8	75

TABLE 2. Micronutrient solutions used in macronutrient experiment

Nutrient	Source	Concentration (mg L^{-1})
Cu	$CuCl_2 \cdot 2H_2O$	0.2
Zn	$ZnCl_2$	0.2
Mn	$MnCl_2 \cdot 4H_2O$	2.0
Mo	$Na_2MoO_4 \cdot 2H_2O$	0.03
B	H_3BO_3	0.5
Fe	FeEDTA	10.0

TABLE 3. Micronutrient treatment concentrations (mg L^{-1})

Nutrient	Source	Level			
		0	1	10	100
Cu	$CuSO_4 \cdot 5H_2O$	0	0.02	0.2	2.0
Zn	$ZnSO_4 \cdot 7H_2O$	0	0.02	0.2	2.0
Mn	$MnCl_2 \cdot 4H_2O$	0	0.05	0.5	5.0
Mo	$Na_2MoO_4 \cdot 2H_2O$	0	0.005	0.05	0.5
B	H_3BO_3	0	0.02	0.2	2.0
Fe	FeEDTA	0	0.4	4.0	40.0

TABLE 4. Macronutrient solutions used in micronutrient experiment

Nutrient	Source	Concentration (mg L^{-1})
N	NH_4NO_3	200
P	KH_2PO_4	50
K		63
K	K_2SO_4	37
S		30
Mg	$MgSO_4 \cdot 7H_2O$	50
S		66
Ca	$CaCl_2 \cdot 2H_2O$	100

Chemical analysis

Samples (described below) were dried for 24 h at 80°C and milled to pass a 40 mesh screen. Approximately 0.15 g of sample was placed in a tin capsule and analysed for total N using a Leco CHN-600 analyser. Sulphur was determined on about 0.25 g of sample using a Leco SC132 analyser. Accuracy of analysis was checked with NBS 1575 pine needle standard, and with in-house standard samples.

The remaining elements were determined on 2.5-g samples which were ashed at 480°C, digested in 2N HCl, filtered, and then analysed on an ARL 3560 OES simultaneous ICAP spectrophotometer. In-house controls were used to ensure accuracy of all elements except B, which was checked with NBS 1573 tomato standard.

Statistical analysis

All data were treated by analysis of variance. The two species were analysed separately, and the model regarded nutrient levels as nested within nutrients. Linear and quadratic contrast terms were then computed for levels within each nutrient. Analysis of heights and dry weights measured in October are presented (Appendix, Tables 11 to 14) to indicate statistical significance of the various treatments.

Macronutrient Experiment 1987

A 3 peat:1 perlite growing medium was used for developing symptoms of N, P, K, Ca, Mg, and S deficiencies. Vermiculite was not used because it releases K, and the peat contained important amounts of Ca and Mg (Appendix, Table 1). Calcium carbonate was incorporated into the medium at 3 kg m^{-3}, except for the Ca treatment series where it was incorporated at 0, 0.30, 0.75, and 3.00 kg m^{-3}. To prevent development of an extremely acid pH, the first three treatments of the Ca series (0, 0.30, and 0.75 kg m^{-3}) received 2 kg m^{-3} of $MgCO_3$.

Stratified seeds of Douglas-fir (seedlot 1292, Stave Lake) and white spruce (seedlot 4284, Prince George) were sown (three seeds per cavity) into the peat/perlite mixture contained in 3-13 styroblocks in a greenhouse at Cowichan Lake Research Station in mid-March 1987. Seedlings were reduced to one per cavity in early April, and nutrient solutions were applied throughout the growing season until October. A 20-h photoperiod was applied to the spruce about 5 weeks after germination, on 17 May, when it was noticed that they were starting to form terminal buds. The seedlings resumed normal growth later in the season as a result of the photoperiod treatment. An 8-h photoperiod was applied to the Douglas-fir for 6 weeks, starting on 1 July, and long photoperiods were switched off over the spruce on 16 July.

Dry weight was determined for 10-seedling samples of Douglas-fir on 2 June, and for 8-seedling samples of white spruce on 16 July. Nutrient concentrations in whole seedlings were then determined by

chemical analysis. Height, stem diameter, and shoot and root dry weights and nutrient concentrations were determined for 20-seedling samples of both species lifted on 19 and 20 October.

Micronutrient Experiment 1988

A perlite growing medium was used in attempting to produce symptoms of Cu, Zn, Mn, Mo, B, and Fe deficiencies. Leaching the perlite with boiling mineral acid showed that important amounts of several nutrients were present (Appendix, Table 2), but the amounts were less than in granular rock wool which was considered as an alternative. Sowing was conducted with the same Douglas-fir seedlot as the macronutrient experiment, and with white spruce (seedlot 4005, Horsefly). Procedures were similar to those in the macronutrient experiment, with sowing in early March and treatments starting in mid-April. Twenty-hour photoperiod was applied to all seedlings from the start of the experiment. An 8-h photoperiod was applied to Douglas-fir seedlings for 3 weeks starting on 2 August, and to white spruce starting on 27 September.

Dry weights of shoots and roots were determined for samples of 15 seedlings lifted on 7 July, and nutrient concentrations of whole seedlings were determined. On 12 October, 20-seedling samples were lifted for determination of height, stem diameter, and shoot and root dry weights and nutrient concentrations.

RESULTS

Macronutrient Experiment

Growth responses to N, P, K, and S treatment levels were obtained (Figure 1; Appendix, Tables 3-6, 11,12). Calcium treatment had no effect, presumably because the quantity of Ca in the peat (0.63%), and in the water supply (0.05 mg L^{-1}) was sufficient for seedling requirements. The apparent small height response to Mg shown by both species (Appendix, Tables 5, 6) was not significant (Appendix, Tables 11, 12). The peat contained 0.17% Mg and this may have been almost adequate for seedling requirements. Nutrient concentrations of whole seedlings associated with maximum dry matter production during the growing period (Appendix, Tables 3, 4) were generally no more than 15% higher than concentrations in shoots associated with maximum dry matter production in October (Figure 1). The main differences were the higher P concentrations of white spruce, the higher S concentrations of Douglas- fir, and the higher K concentrations of both species measured during the growing period.

The apparently negative effect of S on growth of white spruce at the two higher treatment levels (Appendix, Table 4) could have been due to Na toxicity and not to an adverse effect of S. Sulphur was supplied as Na_2SO_4, and it is not unlikely that white spruce, a species which grows inland, is more sensitive to Na than coastal Douglas-fir.

Deficiency symptoms for N, P, K and S were obtained (Figures 3-19; Table 5) and the minimum nutrient concentrations expected in whole seedlings after about 12 weeks growth were estimated (Table 6)

Micronutrient Experiment

Some effect of each of the six micronutrients on height or dry weight was detected in Douglas-fir and white spruce, except that Douglas-fir showed no effect of Cu or Mn (Figure 2; Appendix, Tables 7-10, 13, 14). Only height growth of white spruce was significantly affected by Cu and Mo. Relatively large effects of Zn, Mo, B, and Fe on growth were obtained. The experiment may not have been sufficiently sensitive to detect a significant effect of Mn on Douglas-fir, although there may have been one (Figure 2, Manganese). The critical level for Cu is generally put at 3-4 mg kg^{-1} (Strullu and Bonneau 1978), and Cu contamination and Cu in the seed appear to have been adequate to prevent deficiency symptoms developing. Copper deficiency in container nurseries has certainly been encountered, and when a number of full-sib Douglas-fir families were grown under the same nutrient regime (in work unrelated to the present experiments), development of Cu deficiency symptoms varied greatly according to family.

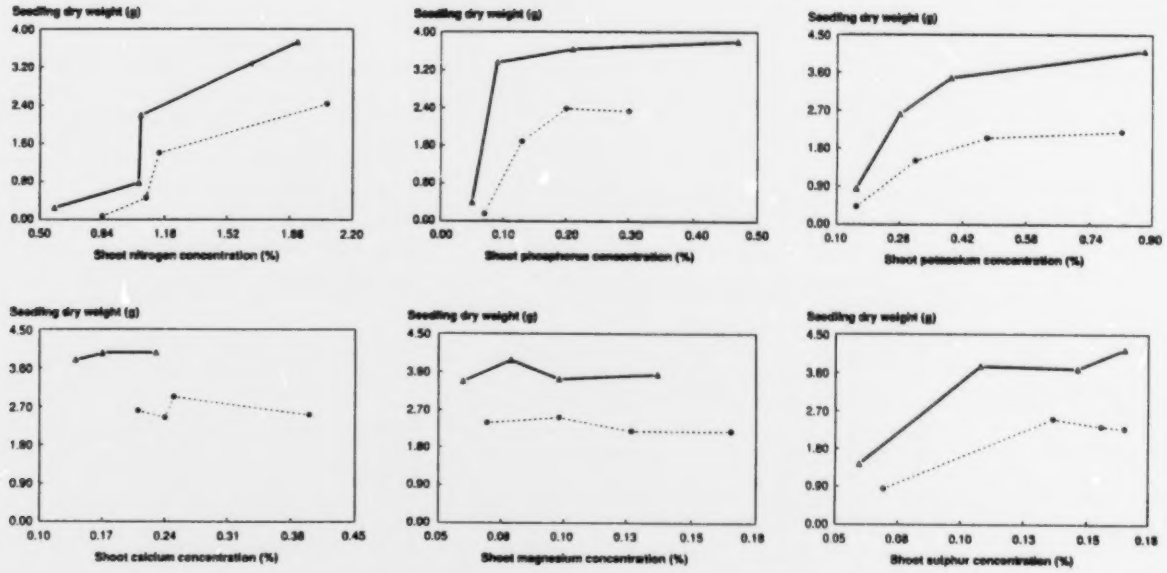
Seedling dry weight (g)
Shoot nitrogen concentration (%)
Shoot phosphorus concentration (%)
Shoot potassium concentration (%)
Shoot calcium concentration (%)
Shoot magnesium concentration (%)
Shoot sulphur concentration (%)

FIGURE 1. Graphs of relationship between whole seedling dry weight and concentrations of macronutrients in shoots in October (Douglas-fir —△— ; White spruce — ●—).

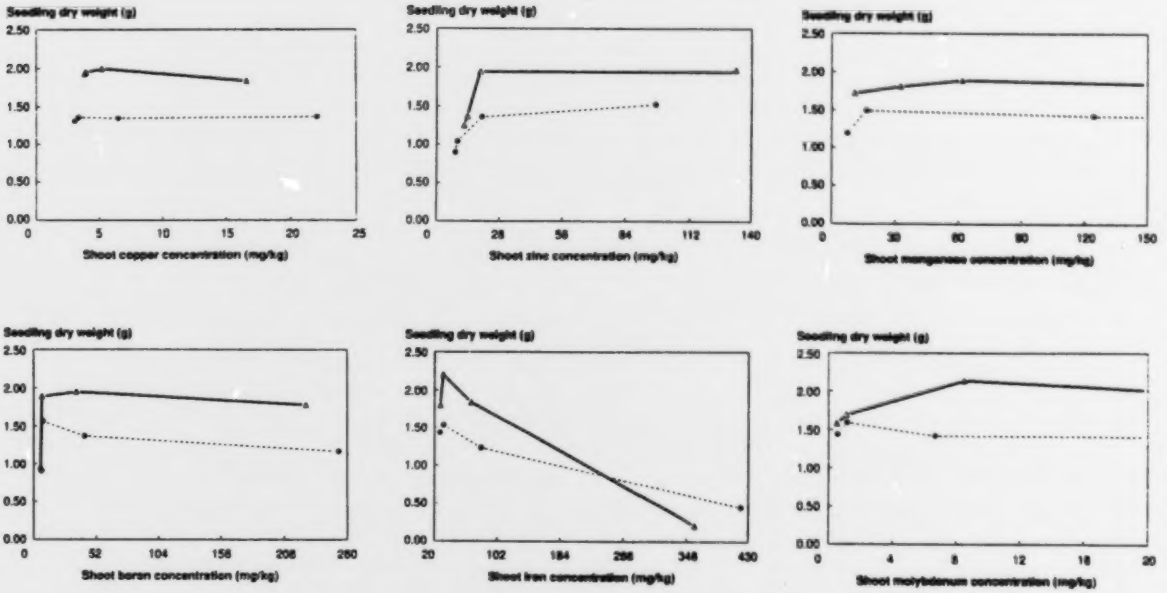
Seedling dry weight (g)
Shoot copper concentration (mg/kg)
Shoot zinc concentration (mg/kg)
Shoot manganese concentration (mg/kg)
Shoot boron concentration (mg/kg)
Shoot iron concentration (mg/kg)
Shoot molybdenum concentration (mg/kg)

FIGURE 2. Graphs of relationship between whole seedling dry weight and concentrations of micronutrients in shoots in October (Douglas-fir —△— ; White spruce — ●—).

TABLE 5. Visual symptoms observed in Douglas-fir and white spruce grown under nutrient-deficient conditions

Nutrient	Deficiency symptoms	
	Douglas-fir	White spruce
N	Needles pale yellow becoming brown at the tip and eventually dying.	Some yellowing at tips of needles leading to red/brown needle development.
P	Dull, greyish, coloured foliage.	Bright purple foliage, gradually turning darker.
K	Seedlings pale green, lower needles yellow towards tips, tips brown.	Seedlings dull green, lower needles first purple at tips, then turning yellow/brown.
S	Yellow needles, as with N deficiency, but severe needle twisting was a distinguishing feature (in the seedlot examined).	No obvious symptoms early in season, later needle extremities become golden, particularly near shoot apex.
Cu	Yellowing or chlorosis of needles, in older seedlings there may be contrast between greener old foliage and pale new foliage. Needles often twisted with terminal spiral.	
Zn	Spiraling of pale terminal needles in early stages. Stunted growth with abnormal needle expansion. Apical needles twisted together, occasionally chlorotic or dead. Foliage colour normal.	Stunted growth with occasional dead needle tips towards shoot apex. Foliage colour otherwise normal.
Mn	Reduced growth, colour normal.	Reduced growth, pale, slightly grey colour. Needles behind apices turning yellow over whole length and dying.
B	Stunted growth, few branches. Terminal bud small or absent. Needles near apex reduced or absent.	Stunted growth, terminal buds small or absent. Apical needles short, twisted, and necrotic.
Fe	Terminal needles pale green to white, occasional spiraling of apical needles. Overall colour pale yellow green.	Needles near shoot apex pale green, sometimes showing yellow tips. Overall colour normal.

Deficiency symptoms attributable to Mo deficiency, or to Mn deficiency in Douglas-fir were not seen (Table 5). Minimum trace element concentrations to be expected in 12-week-old seedlings were also estimated (Table 6).

The fourth level of micronutrient was applied at 10 times the level generally supposed to be optimal, to look for toxic effects. The micronutrient showing the greatest toxicity was Fe (Appendix, Tables 9-10; Figure 2, Iron; Figures 23, 29). Both 4.0 and 40 mg L^{-1} reduced growth compared with 0.4 mg L^{-1}, although there was a response at this latter level over control. Copper at 2.0 mg L^{-1} produced marked toxicity symptoms on white spruce by October (Figure 34). Ends of needles died and turned brown, in some cases over the whole seedling. The higher levels of B also appeared to reduce growth a little, particularly of white spruce. In contrast, the highest level of Zn (2.0 mg L^{-1}) increased growth of white spruce (Appendix, Table 10; Figure 2, Zinc). The optimum Zn supply for growth was probably somewhere in the range of 0.2 to 2.0 mg L^{-1}, and the straight line used for joining the points (Figure 2) probably does not depict the true relationship.

There were considerable differences in micronutrient concentrations between analyses made in July and October (Appendix, Tables 7-10). In general, concentrations in the low levels of treatment decreased between July and October, while concentrations in the high levels of treatment increased in this time interval. At high levels of supply, Mn accumulated in shoots, particularly in white spruce, whereas Mo accumulated in roots. Shoot Mo concentrations were low and differentiation between treatments difficult, so that root or whole seedling analysis appeared to be the best way of examining the status of this element (Figure 2, Molybdenum).

TABLE 6. Minimal nutrient concentrations expected in Douglas-fir and white spruce container seedlings after about 12 weeks' growth

Nutrient	Douglas-fir	White spruce
N %	2.2	2.5
P %	0.25	0.4
K %	0.9	1.0
Ca %	0.12	0.2
Mg %	0.12	0.12
S %	0.22	0.14
Cu mg kg^{-1}*	9[a]	15[a]
Zn mg kg^{-1}	30	33
Mn mg kg^{-1}	20	19
Mo mg kg^{-1}	4	0.5
B mg kg^{-1}	42	46
Fe mg kg^{-1}	40	50

* mg kg^{-1} = parts per million (ppm).

[a] 4 mg kg^{-1} is the generally recognized minimal concentration for Cu in conifer foliage, but higher values could be expected in whole seedlings as a result of higher root concentrations.

CONCLUSIONS

Nutrient deficiency symptoms in young Douglas-fir and white spruce develop at very low nutrient supply levels, and are often only subtly different between elements. Growth reduction is always severe before symptoms develop and it is necessary to obtain a complete chemical analysis before reaching a conclusion about the cause of symptoms. Microelement toxicity, such as that due to Fe and Cu observed in this work, should always be considered as a cause of symptoms.

The high levels of macronutrients used in this work (N = 200, P = 50, K = 100, and S = 75 mg L^{-1} of nutrient solution) are suitable for producing adequate seedlings when applied twice a week. In operational practice, lower concentrations are used and nutrient solutions are applied more frequently (e.g., Tinus and McDonald 1979). Calcium and Mg requirements for seedling production appear to be low. They may actually be satisfied by the Ca and Mg present in the peat and water supply. Calcium and Mg deficiencies are unlikely to occur when 3 kg of dolomitic lime is mixed in per cubic metre of peat and vermiculite growing medium.

Micronutrient concentrations required in nutrient solutions to obtain satisfactory growth appeared to be Cu = 0.2, Zn = 0.2 (perhaps as high as 2.0 for white spruce), Mn = 0.5, Mo = 0.05, B = 0.2, and Fe = 0.4 mg L^{-1}. Growth on the pure perlite medium in the micronutrient experiment was inferior to that obtained on the peat/perlite mixture with similar nutrition in the macronutrient experiment. Perlite does not retain water as well as peat, so that seedlings probably experienced more water stress, and perhaps received less nutrients because of more rapid drainage.

Previous analyses showed that commercial soluble fertilizers used in British Columbia contain 900-3000 mg Fe kg^{-1} and 17-20% N[2]. Preparation of a nutrient solution containing 200 mg N L^{-1} from these fertilizers would result in Fe concentrations of 1.0-3.5 mg Fe L^{-1}. The latter concentration might be too high for optimal growth. When abundant Fe is already being supplied, the addition of $FeSO_4$ (a common practice in operational nurseries) could result in toxic concentrations of Fe in some instances. The beneficial effects of $FeSO_4$ are almost always due to the S supplied. Provided adequate S can be supplied in some other way (as $(NH_4)_2SO_4$ or K_2SO_4) , use of $FeSO_4$ might best be avoided.

Concentrations of N, P, and K considered desirable for actively growing seedlings (Table 5) were higher than concentrations thought to represent adequate nutrition in needles of older dormant trees (Ballard and Carter 1986). A lower proportion of structural material in young seedling shoots, as well as seasonal differences, could explain this discrepancy. The critical level of Ca may actually be higher in needles from older dormant trees than it is in seedlings. Calcium accumulates, particularly in cell walls, and the requirement in succulent young seedlings is probably relatively low. Concentrations of micronutrients proposed as desirable for actively growing seedlings (Table 5) were considerably higher than critical values given for needles of dormant trees (Ballard and Carter 1986).

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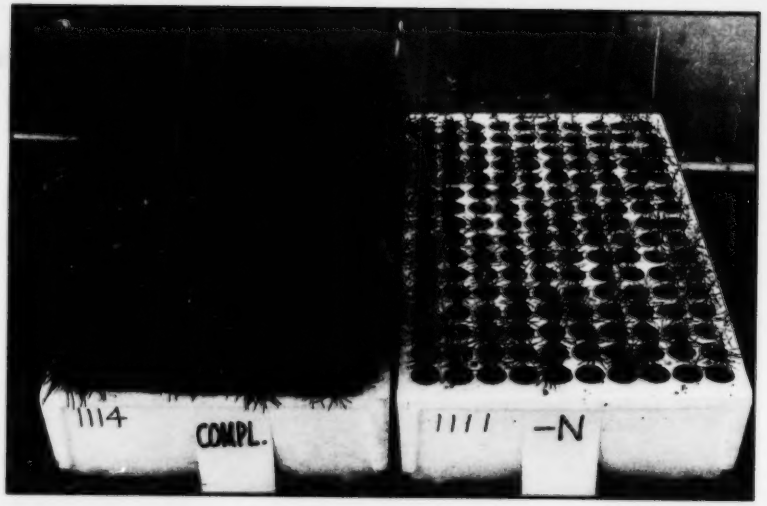

FIGURE 3. Blocks of Douglas-fir grown with complete nutrition and without nitrogen (–N), July.

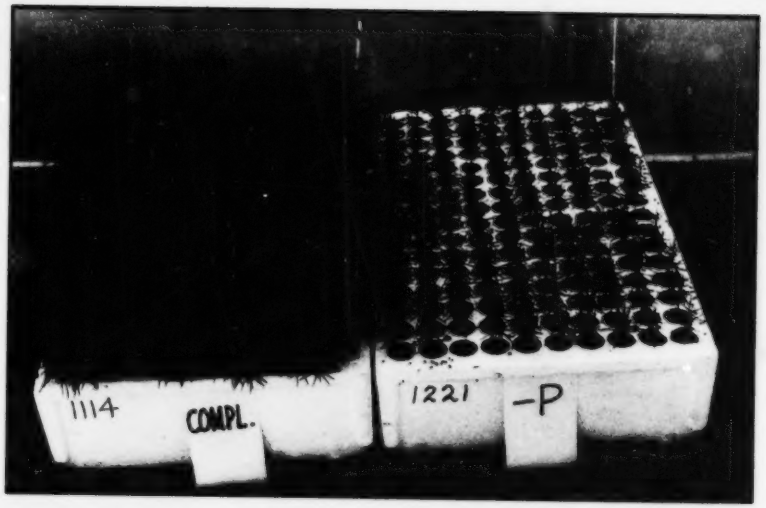

FIGURE 4. Blocks of Douglas-fir grown with complete nutrition and without phosphorus (–P), July.

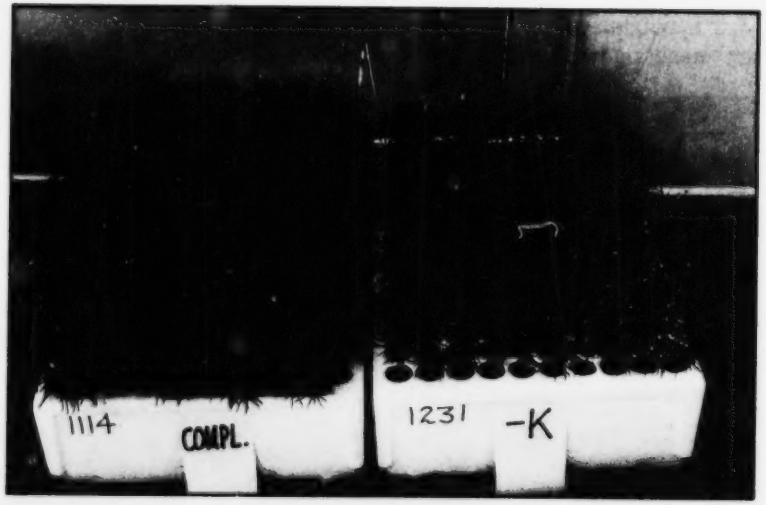

FIGURE 5. Blocks of Douglas-fir grown with complete nutrition and without potassium (–K), July.

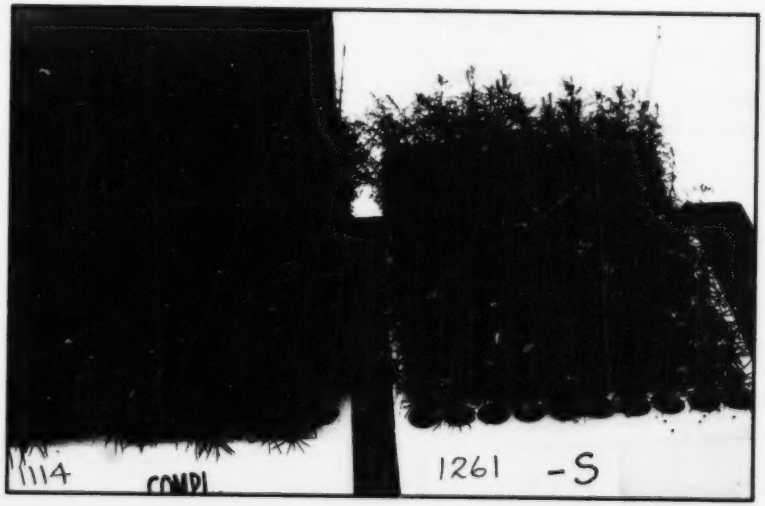

FIGURE 6. Blocks of Douglas-fir grown with complete nutrition and without sulphur (–S), July.

FIGURE 7. Douglas-fir seedlings grown at four nitrogen levels, 200 (compl), 50, 20 and 0 (–N) mg L^{-1}, photographed in July.

FIGURE 8. Douglas-fir grown with sulphur at 75 mg L^{-1} (compl) and without sulphur (–S), photographed in July.

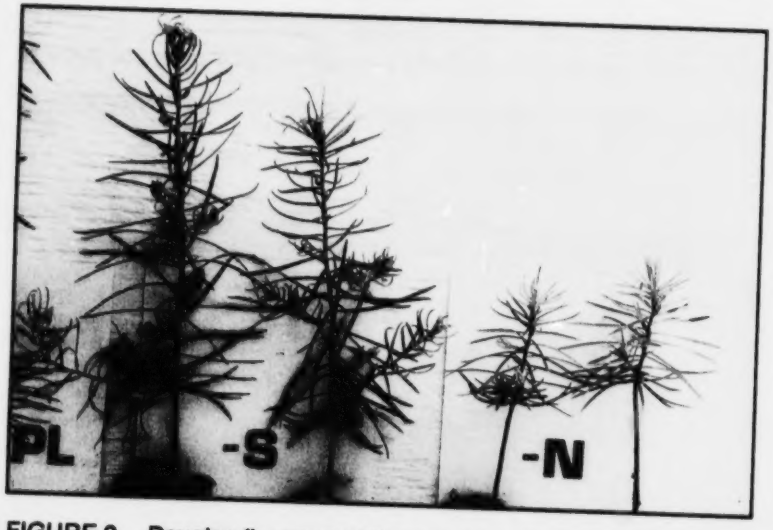

FIGURE 9. Douglas-fir grown with no sulphur (–S) and no nitrogen (–N), photographed in July. Note curling of sulphur-deficient needles.

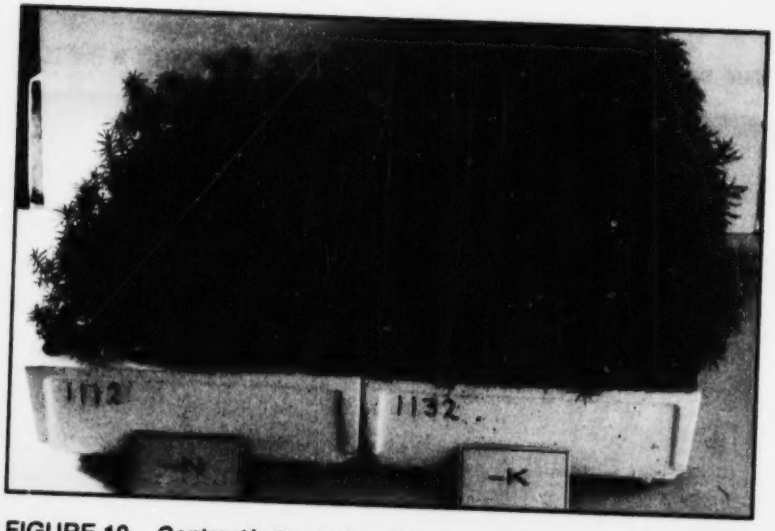

FIGURE 10. Contrast between low nitrogen and low potassium. Blocks of Douglas-fir grown at 20 mg L^{-1} nitrogen (–N) and 10 mg L^{-1} potassium (–K), photographed in October.

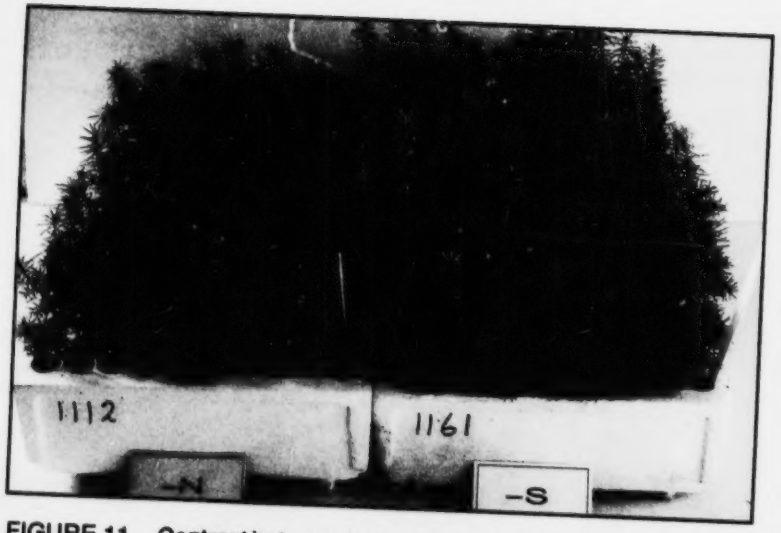

FIGURE 11. Contrast between low nitrogen and low sulphur. Blocks of Douglas-fir grown at 20 mg L^{-1} nitrogen (–N) and 0 mg L^{-1} sulphur (–S), photographed in October.

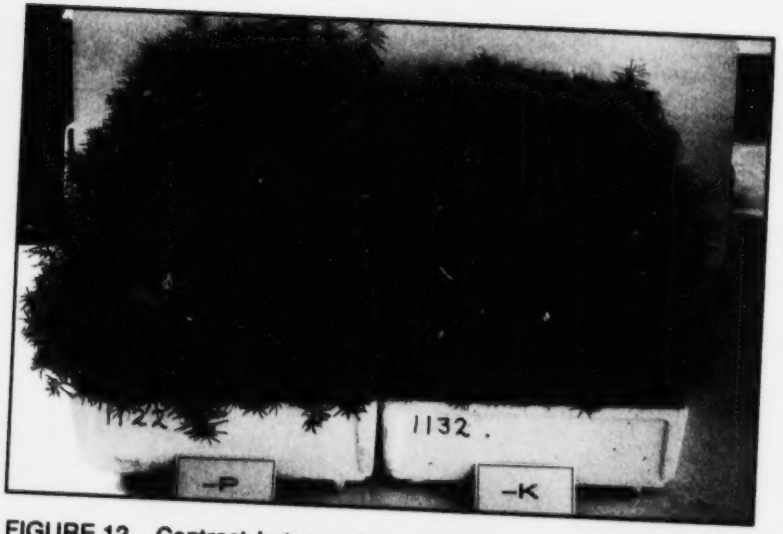

FIGURE 12. Contrast between low phosphorus and low potassium. Blocks of Douglas-fir grown at 5 mg L^{-1} phosphorus (–P) and 10 mg L^{-1} potassium (–K), photographed in October.

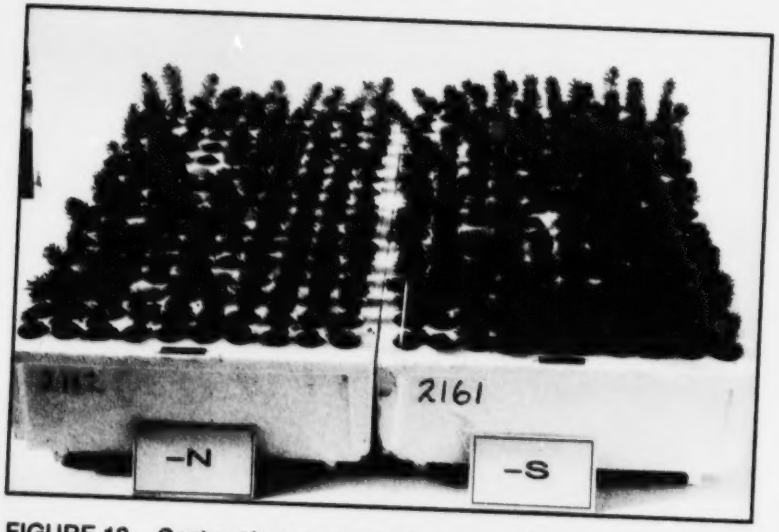

FIGURE 13. Contrast between low nitrogen and low sulphur. Blocks of white spruce grown at 20 mg L^{-1} nitrogen (–N) and 0 mg L^{-1} sulphur (–S), photographed in October.

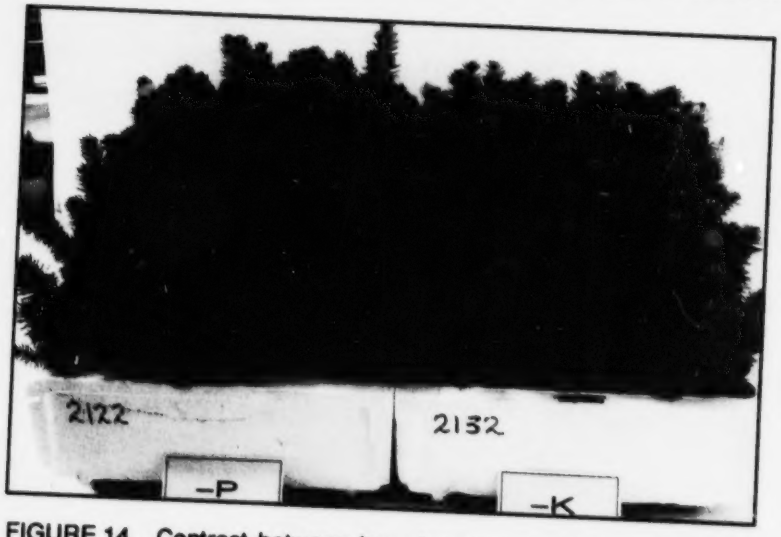

FIGURE 14. Contrast between low phosphorus and low potassium. Blocks of white spruce grown at 5 mg L^{-1} phosphorus (–P) and 10 mg L^{-1} potassium (–K), photographed in October.

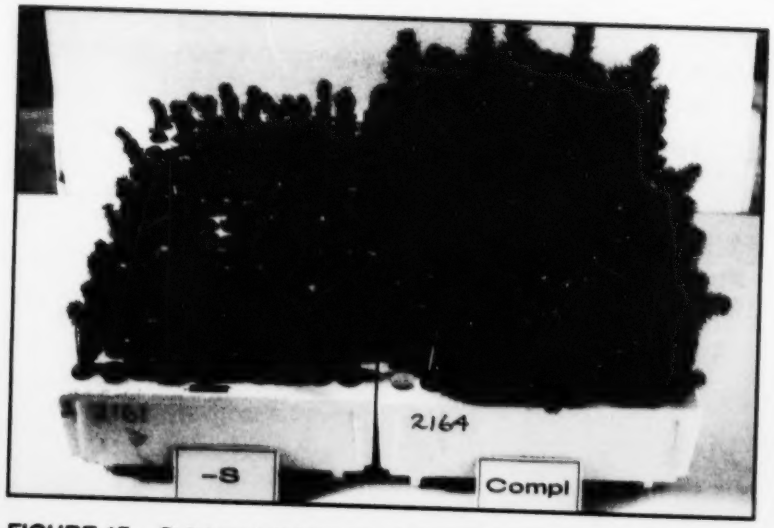

FIGURE 15. Sulphur deficiency in white spruce. Blocks of white spruce grown at 0 mg L^{-1} sulphur (–S) and 75 mg L^{-1} sulphur (compl), photographed in October.

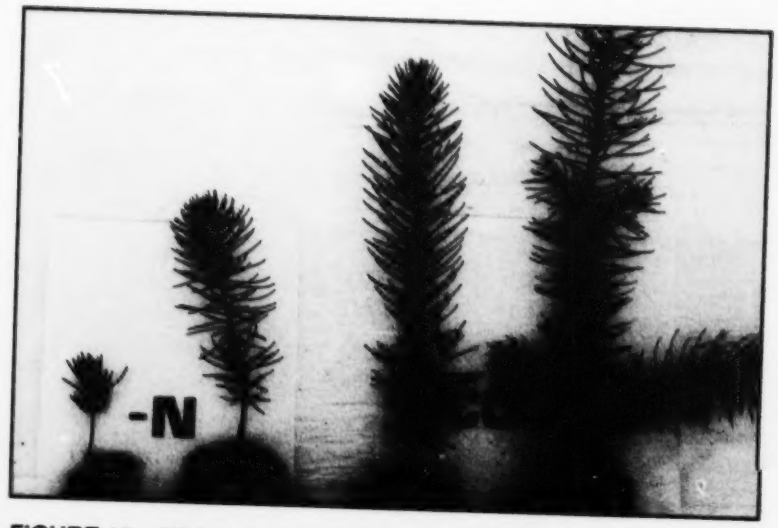

FIGURE 16. White spruce grown at 0 (–N), 20, 50 and 200 (compl) mg nitrogen L^{-1}, photographed in October.

FIGURE 17. White spruce grown at 0 (–P), 5, 12.5 and 50 (compl) mg phosphorus L^{-1}, photographed in October.

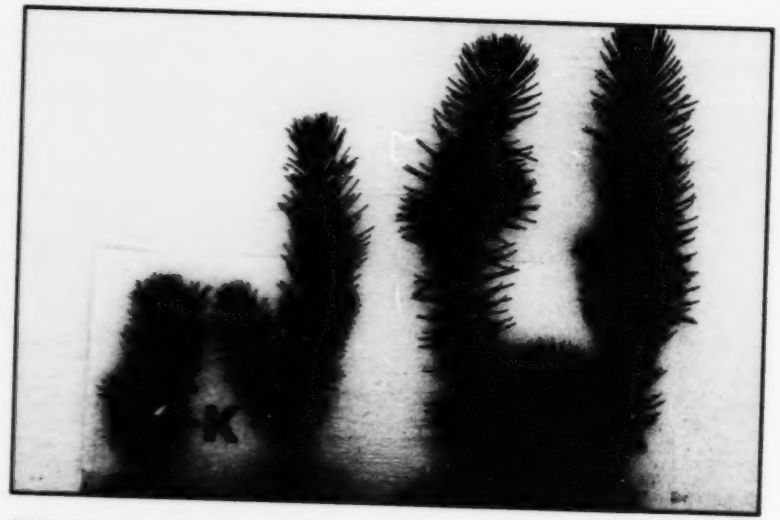

FIGURE 18. White spruce grown at 0 (–K), 10, 25 and 100 (compl) mg potassium L^{-1}, photographed in October.

FIGURE 19. White spruce grown at 0 (–S), 7.5, 18.8 and 75 (compl) mg sulphur L^{-1}, photographed in October.

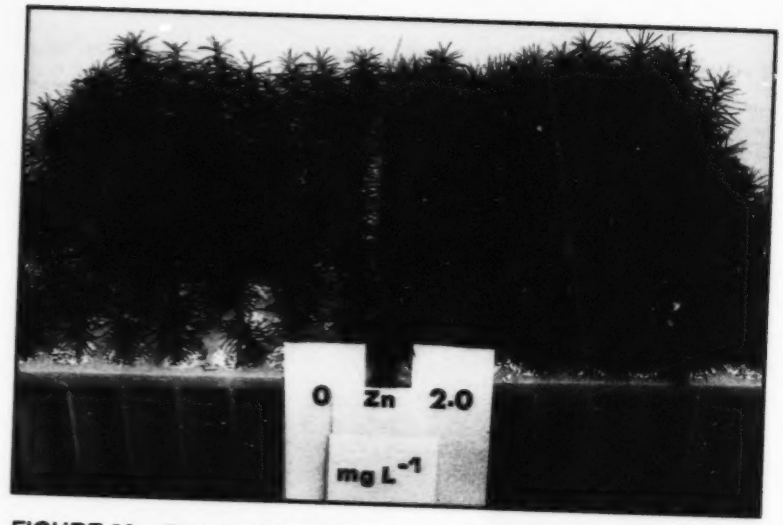

FIGURE 20. Douglas-fir grown with no zinc (0) and 2.0 mg zinc L^{-1}, photographed in June.

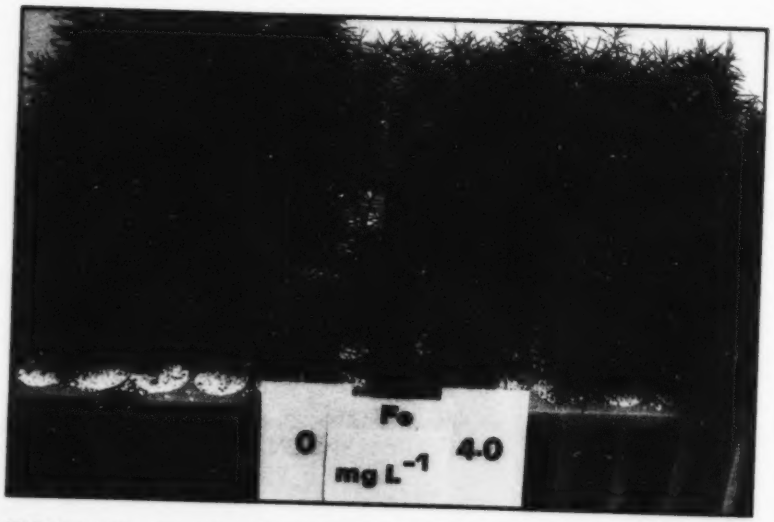

FIGURE 21. Douglas-fir grown with no iron (0) and 4.0 mg iron L^{-1}, photographed in June. Iron supplied as EDTA chelate.

FIGURE 22. Iron deficiency in Douglas-fir during June.

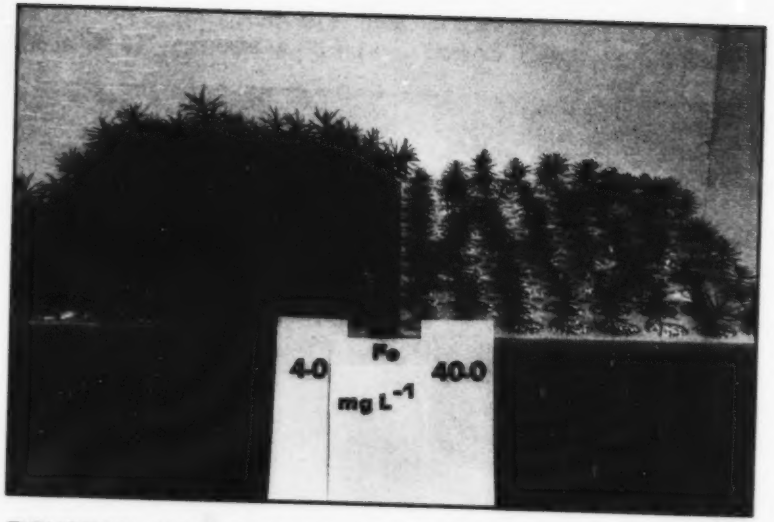

FIGURE 23. Iron toxicity in Douglas-fir receiving 40 mg iron L^{-1} supplied as chelate. Normal, dark green seedlings received 4 mg L^{-1} iron.

FIGURE 24. Iron deficient (0) and normal (0.4 mg iron L^{-1}) Douglas-fir photographed in October.

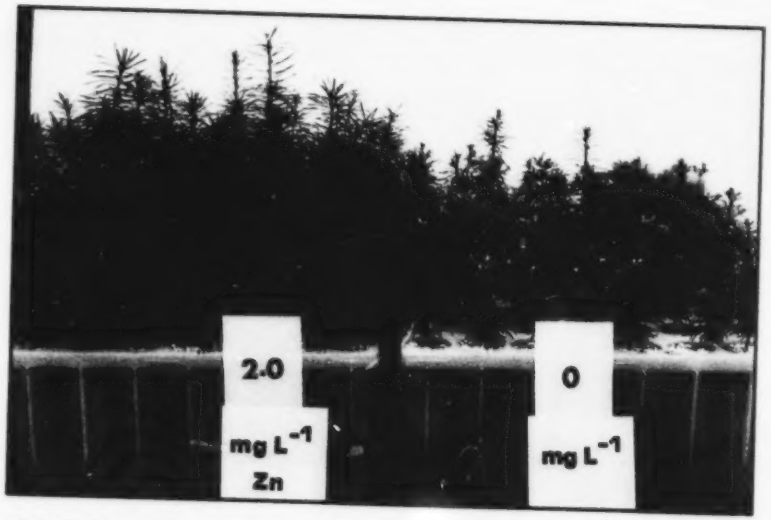

FIGURE 25. Normal (2.0 mg zinc L^{-1}) and zinc-deficient Douglas-fir (0) photographed in October.

FIGURE 26. Close-up of zinc-deficient Douglas-fir photographed in October.

FIGURE 27. Normal (0.02 mg boron L^{-1}) and boron-deficient (0) Douglas-fir photographed in October.

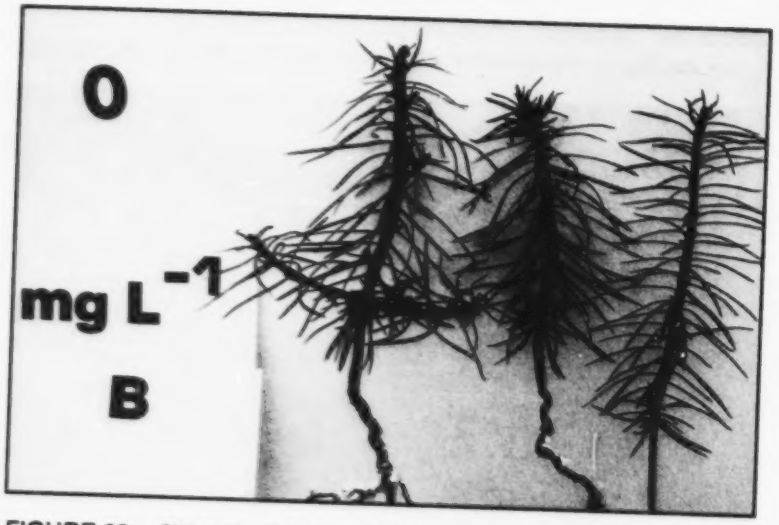

FIGURE 28. Close-up of boron-deficient Douglas-fir photographed in October.

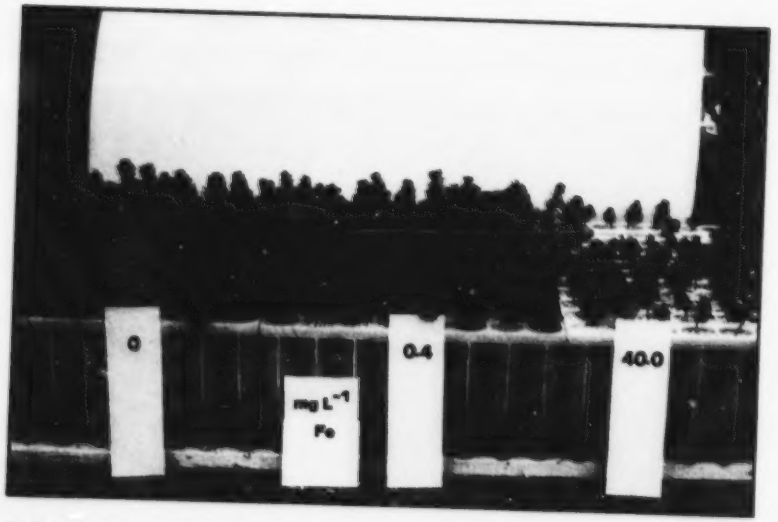

FIGURE 29. Iron toxicity in white spruce. Blocks of white spruce grown at 0, 0.4 and 40.0 mg L^{-1} iron applied as EDTA chelate and photographed in October. There was no difference in growth between 0 and 0.4 mg L^{-1} (see Iron in FIGURE 2).

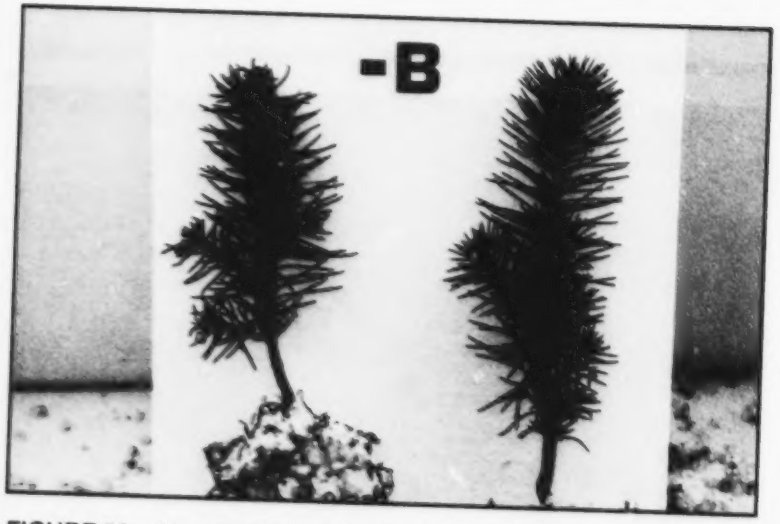

FIGURE 30. Boron-deficient white spruce photographed in October. Damage to apical meristems most evident in seedling on left.

FIGURE 31. Manganese-deficient (0) and normal (5.0 mg manganese L^{-1}) white spruce.

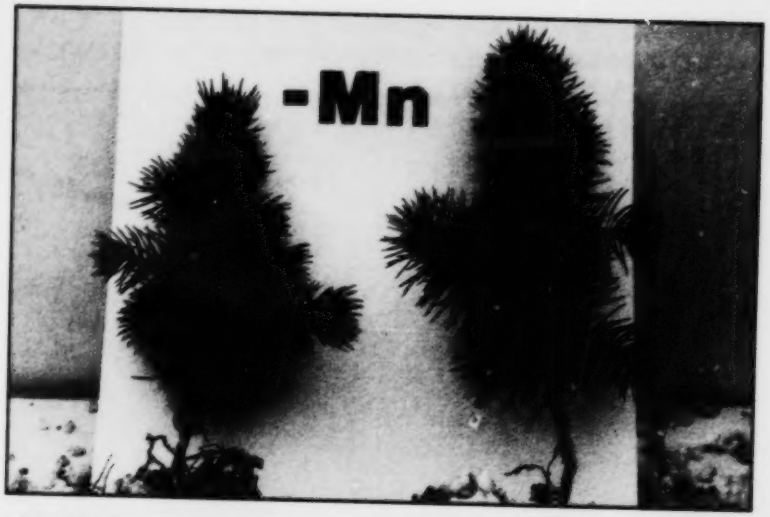

FIGURE 32. Close-up of manganese-deficient seedlings photographed in October.

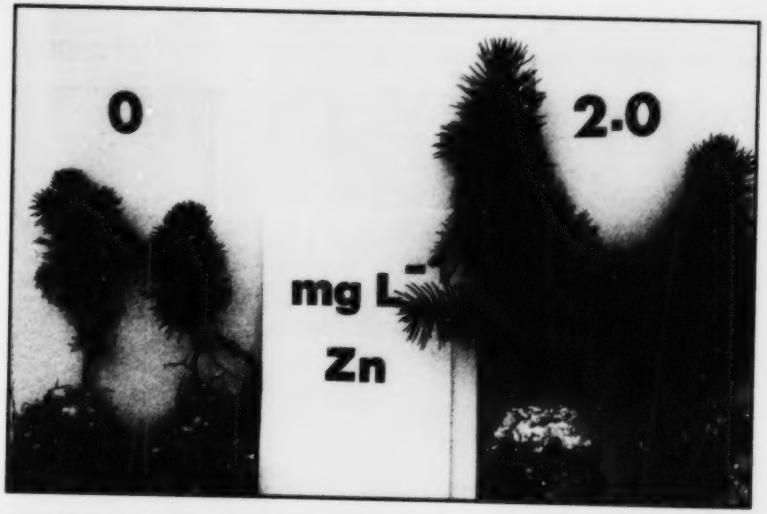

FIGURE 33. Zinc-deficient (0) and normal (2.0 mg zinc L^{-1}) white spruce photographed in October.

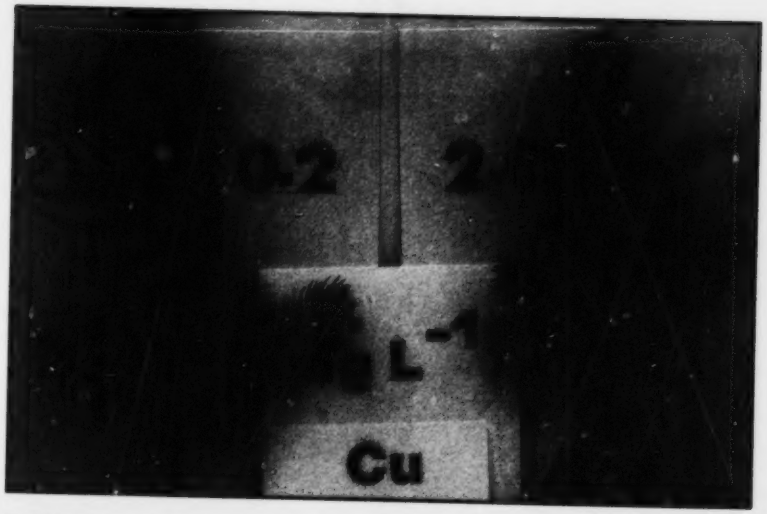

FIGURE 34. Copper toxicity in white spruce receiving 2.0 mg copper L^{-1}, compared with normal seedling receiving 0.2 mg copper L^{-1}, photographed in October.

APPENDIX TABLES

TABLE 1. Concentration of major nutrients in peat used in macronutrient experiment (mg L^{-1})

NH_4–N	NO_3–N	P	K	Ca	Mg	Mn
149	19	13	314	6300	1740	119

TABLE 2. Analysis of perlite leachate (10 g perlite leached three times with 100 mL aliquots boiling 10% HCl) (mg kg^{-1})

P	K	Ca	Mg	Cu	Fe	Mn	Zn	Na	B	Mo	Al	S
2.0	362	153	8	0.06	96	3.0	0.5	681	0	0	265	9

TABLE 3. Douglas-fir mean dry weights and macronutrient concentrations (% whole dry seedling) measured on 2 June after 10 weeks' growth

Nutrient	Level (mg L^{-1})	Dry weight (g)	N	P	K	Ca	Mg	S
					(%)			
N	0	0.15	0.72	0.65	1.25	0.42	0.15	0.21
	20	0.19	1.01	0.84	1.62	0.41	0.18	0.22
	50	0.33	1.51	0.80	1.74	0.40	0.18	0.26
	200	0.46	2.20	0.73	1.56	0.32	0.15	0.21
P	0	0.16	2.69	0.09	0.76	0.31	0.13	0.20
	5	0.46	2.21	0.24	1.29	0.32	0.14	0.23
	12.5	0.43	2.24	0.55	1.57	0.32	0.15	0.25
	50	0.43	2.21	0.70	1.58	0.32	0.15	0.26
K	0	0.25	2.22	0.81	0.24	0.40	0.19	0.25
	10	0.42	2.25	0.71	0.54	0.41	0.19	0.25
	25	0.47	2.20	0.74	0.89	0.43	0.18	0.24
	100	0.49	2.20	0.65	1.51	0.32	0.15	0.25
Ca	0 [a]	0.50	2.53	0.81	1.51	0.12	0.30	0.27
	1	0.44	2.32	0.75	1.53	0.14	0.28	0.28
	2.5	0.48	2.24	0.80	1.59	0.16	0.27	0.26
	10	0.48	2.13	0.72	1.62	0.40	0.15	0.26
Mg	0	0.44	2.40	0.84	1.68	0.38	0.12	0.26
	5	0.47	2.31	0.79	1.64	0.36	0.12	0.26
	12.5	0.42	2.22	0.80	1.68	0.36	0.12	0.26
	50	0.41	2.14	0.78	1.72	0.32	0.15	0.27
S	0	0.28	3.25	1.05	1.36	0.41	0.17	0.10
	7.5	0.44	2.22	0.70	1.61	0.33	0.16	0.20
	18.8	0.45	2.25	0.72	1.60	0.37	0.16	0.22
	75	0.43	2.37	0.75	1.66	0.36	0.16	0.26

[a] See text for Ca levels.

TABLE 4. White spruce mean dry weights and macronutrient concentrations (% whole dry seedling) measured on 16 July after 16 weeks' growth

Nutrient	Level (mg L^{-1})	Dry weight (g)	N	P	K	Ca	Mg	S
					(%)			
N	0	0.04	0.77	*	*	*	*	0.08
	20	0.21	1.12	0.40	1.32	0.48	0.22	0.09
	50	0.39	1.39	0.40	1.50	0.45	0.23	0.10
	200	0.78	2.46	0.43	1.53	0.40	0.19	0.19
P	0	0.09	2.65	*	*	*	*	0.09
	5	0.40	2.22	0.16	1.33	0.37	0.16	0.13
	12.5	0.54	2.33	0.24	1.36	0.36	0.17	0.16
	50	0.80	2.49	0.39	1.47	0.41	0.18	0.14
K	0	0.26	2.72	0.55	0.20	0.36	0.19	0.17
	10	0.37	2.50	0.50	0.45	0.36	0.20	0.19
	25	0.66	2.48	0.46	0.68	0.36	0.21	0.20
	100	0.77	2.33	0.42	1.46	0.36	0.19	0.17
Ca	0 [a]	0.70	2.43	0.45	1.83	0.20	0.26	0.19
	1	0.64	2.40	0.47	1.57	0.26	0.31	0.18
	2.5	0.74	2.37	0.45	1.63	0.25	0.30	0.16
	10	0.58	2.59	0.43	1.88	0.47	0.20	0.17
Mg	0	0.55	2.66	0.46	1.66	0.43	0.10	0.18
	5	0.50	2.49	0.44	1.55	0.35	0.11	0.17
	12.5	0.42	2.87	0.46	1.71	0.12	0.14	0.17
	50	0.53	2.64	0.43	1.66	0.37	0.18	0.17
S	0	0.38	2.59	0.52	1.13	0.40	0.19	0.07
	7.5	0.80	2.47	0.44	1.52	0.39	0.18	0.13
	18.8	0.61	2.75	0.44	1.44	0.37	0.16	0.14
	75	0.58	2.69	0.43	1.33	0.35	0.24	0.18

* Insufficient sample for analysis.
[a] See text for Ca levels.

TABLE 5. Morphological measurements and shoot and root concentrations of macronutrient varied in treatment for Douglas-fir measured on 20 October

Nutrient	Level ($mg\ L^{-1}$)	Height (cm)	Stem diameter (mm)	Shoot/root dry wt ratio	Nutrient concentration	
					Shoot %	Root %
N	0	6.0	1.2	0.74	0.58	0.36
	20	11.3	2.0	0.85	1.04	0.70
	50	20.3	3.2	1.26	1.05	0.76
	200	29.7	4.0	2.02	1.90	1.38
P	0	7.3	1.4	1.13	0.05	0.06
	5	25.8	3.6	1.90	0.09	0.09
	12.5	30.5	3.9	2.32	0.21	0.16
	50	30.5	4.1	2.22	0.47	0.32
K	0	11.1	2.3	2.53	0.15	0.16
	10	22.3	3.5	2.22	0.26	0.19
	25	27.7	3.9	2.20	0.39	0.31
	100	30.0	4.2	1.93	0.88	0.89
Ca	0 [a]	30.4	4.1	2.39	0.14	0.13
	1	30.2	4.2	2.24	0.17	0.16
	2.5	30.7	4.1	2.24	0.17	0.15
	10	31.1	4.1	2.25	0.23	0.21
Mg	0	27.9	3.7	1.93	0.06	0.04
	5	28.7	4.1	1.98	0.08	0.06
	12.5	29.0	3.8	2.06	0.10	0.07
	50	29.3	3.9	2.25	0.14	0.10
S	0	19.3	2.4	1.70	0.06	0.07
	7.5	29.7	4.0	2.26	0.11	0.08
	18.8	30.2	4.0	2.20	0.15	0.12
	75	30.5	4.1	2.08	0.17	0.15

[a] See text for Ca levels.

TABLE 6. Morphological measurements and shoot and root concentrations of macronutrient varied in treatment for white spruce measured on 20 October

Nutrient	Level ($mg\ L^{-1}$)	Height (cm)	Stem diameter (mm)	Shoot/root dry wt ratio	Nutrient concentration	
					Shoot %	Root %
N	0	2.2	0.6	0.58	0.84	0.80
	20	5.4	1.3	0.72	1.08	0.83
	50	11.7	2.1	0.97	1.15	0.94
	200	18.7	3.0	1.96	2.06	1.69
P	0	3.6	1.0	1.65	0.07	0.09
	5	14.8	2.5	1.86	0.13	0.10
	12.5	17.5	2.9	1.92	0.20	0.15
	50	18.3	3.0	2.10	0.30	0.27
K	0	6.4	1.7	4.23	0.15	0.20
	10	13.4	2.6	2.53	0.30	0.26
	25	15.2	2.9	1.97	0.48	0.37
	100	17.0	2.8	1.78	0.82	0.69
Ca	0 [a]	19.9	3.2	2.14	0.21	0.14
	1	18.7	3.1	2.05	0.24	0.16
	2.5	20.3	3.3	2.00	0.25	0.15
	10	19.0	3.0	2.06	0.40	0.20
Mg	0	17.6	2.9	1.75	0.07	0.05
	5	18.9	2.9	1.80	0.10	0.07
	12.5	19.0	2.8	2.12	0.13	0.09
	50	20.1	2.8	2.19	0.17	0.12
S	0	8.2	1.8	1.08	0.07	0.07
	7.5	18.8	3.1	2.00	0.14	0.12
	18.8	19.4	3.1	2.39	0.16	0.18
	75	17.6	2.9	2.20	0.17	0.19

[a] See text for Ca levels.

TABLE 7. Douglas-fir mean dry weights and micronutrient concentrations (% whole dry seedling) measured on 7 July after 12 weeks' growth

Nutrient	Level ($mg\ L^{-1}$)	Dry weight (g)	Cu	Zn	Mn	Mo	B	Fe
					($mg\ kg^{-1}$)			
Cu	0	0.50	9.1	21.6	50.5	4.2	55.6	82.3
	0.02	0.63	11.3	20.1	34.7	4.1	56.4	89.9
	0.2	0.64	14.8	27.4	35.8	3.5	55.7	90.1
	2.0	0.60	42.8	20.5	37.9	4.4	50.2	77.4
Zn	0	0.54	24.4	14.1	45.8	4.9	64.2	108.6
	0.02	0.49	28.5	14.2	38.8	4.3	51.9	90.6
	0.2	0.58	22.1	30.0	33.4	3.8	55.9	78.9
	2.0	0.63	18.1	65.6	37.6	4.1	52.5	80.1
Mn	0	0.51	14.4	21.7	21.5	3.7	53.9	77.0
	0.05	0.59	16.9	20.6	12.1	3.7	52.5	83.3
	0.5	0.57	12.0	19.2	35.2	3.5	50.1	74.5
	5.0	0.48	25.7	20.4	224.1	4.0	54.1	82.3
Mo	0	0.53	18.2	18.4	36.5	0.3	54.8	80.0
	0.005	0.57	16.2	19.4	35.3	0.5	60.8	85.0
	0.05	0.64	17.0	21.7	46.4	4.1	51.8	80.1
	0.5	0.47	25.7	20.8	50.2	43.4	60.5	84.9
B	0	0.45	52.6	20.4	58.8	5.9	33.4	81.7
	0.02	0.54	32.5	20.9	59.2	4.5	41.8	86.1
	0.2	0.61	15.2	21.9	35.6	3.9	52.4	87.7
	2.0	0.60	30.2	20.2	36.3	4.4	171.7	88.3
Fe	0	0.58	25.2	26.8	2.3	4.4	61.5	32.8
	0.4	0.65	26.9	23.5	23.5	3.8	57.5	39.0
	4.0	0.63	18.9	19.1	2.7	3.8	53.3	79.0
	40.0	0.12	56.7	24.3	1.1	4.6	62.3	325.7

TABLE 8. White spruce mean dry weights and micronutrient concentrations (% whole dry seedling) measured on 7 July after 12 weeks' growth

Nutrient	Level (mg L^{-1})	Dry weight (g)	Cu	Zn	Mn	Mo	B	Fe
					(mg kg^{-1})			
Cu	0	0.30	15.0	28.3	59.5	3.9	63.2	83.5
	0.02	0.27	18.9	28.5	58.2	4.5	63.3	86.8
	0.2	0.27	38.9	31.8	79.5	4.8	64.0	85.1
	2.0	0.29	35.8	28.2	52.5	4.7	57.6	82.1
Zn	0	0.25	38.7	21.8	120.0	5.2	70.8	90.4
	0.02	0.26	30.3	20.7	67.9	5.1	64.8	92.6
	0.2	0.27	50.1	32.7	68.4	4.7	64.5	82.7
	2.0	0.26	31.9	85.9	61.9	4.5	64.0	86.9
Mn	0	0.24	32.8	42.5	16.4	4.7	74.4	95.4
	0.05	0.23	21.1	31.5	18.6	4.0	62.7	85.1
	0.5	0.31	14.5	28.7	100.3	4.2	67.8	75.8
	5.0	0.27	12.2	30.9	324.3	4.1	62.7	75.5
Mo	0	0.28	15.5	28.1	93.3	0.3	58.3	75.6
	0.005	0.29	48.0	38.0	93.3	0.5	55.2	85.4
	0.05	0.28	33.1	34.4	63.9	4.1	62.9	88.5
	0.5	0.25	37.1	31.9	64.3	61.5	65.2	99.3
B	0	0.23	15.0	31.9	75.4	8.5	49.8	89.0
	0.02	0.31	18.9	30.6	90.9	5.0	45.9	85.0
	0.2	0.26	38.9	30.7	68.1	4.8	56.7	90.3
	2.0	0.26	35.8	30.9	71.5	4.7	173.9	84.7
Fe	0	0.24	18.9	36.1	77.9	4.8	76.0	42.5
	0.4	0.25	18.0	34.6	103.5	4.0	65.4	50.0
	4.0	0.28	28.1	30.1	60.3	5.0	62.2	89.0
	40.0	0.12	19.4	34.5	64.3	6.0	66.9	344.7

TABLE 9. Morphological measurements and shoot and root concentrations of micronutrient varied in treatment for Douglas-fir measured on 12 October

Nutrient	Level ($mg\ L^{-1}$)	Height (cm)	Stem diameter (mm)	Shoot/root dry wt ratio	Nutrient concentration	
					Shoot %	Root %
Cu	0	19.2	2.6	2.43	3.8	5.5
	0.02	18.1	2.3	2.24	3.9	7.1
	0.2	19.4	2.5	2.48	5.2	14.7
	2.0	18.5	2.4	2.09	16.6	98.2
Zn	0	10.8	2.1	1.45	12.3	20.7
	0.02	13.4	2.1	1.68	13.8	24.4
	0.2	19.0	2.4	2.30	19.5	53.2
	2.0	19.3	2.5	2.46	132.9	111.7
Mn	0	17.5	2.3	2.31	32.5	9.5
	0.05	17.5	2.4	2.34	10.9	6.1
	0.5	17.2	2.4	2.49	61.8	15.2
	5.0	17.4	2.3	2.32	471.2	99.1
Mo	0	16.9	2.2	2.32	0.32	0.51
	0.005	18.6	2.2	2.22	0.22	1.11
	0.05	19.8	2.5	2.21	0.41	8.49
	0.5	17.0	2.3	2.23	2.12	71.23
B	0	11.8	1.8	2.22	5.7	16.7
	0.02	18.9	2.5	2.27	7.0	11.7
	0.2	19.1	2.5	2.09	35.5	17.2
	2.0	18.7	2.5	2.59	225.9	46.4
Fe	0	18.9	2.3	2.07	27.8	37.7
	0.4	20.9	2.7	2.37	31.4	55.3
	4.0	18.7	2.6	2.34	68.2	155.6
	40.0	5.8	1.2	1.90	358.5	364.6

TABLE 10. Morphological measurements and shoot and root concentrations of micronutrient varied in treatment for white spruce measured on 12 October.

Nutrient	Level ($mg\ L^{-1}$)	Height (cm)	Stem diameter (mm)	Shoot/root dry wt ratio	Nutrient concentration	
					Shoot %	Root %
Cu	0	10.4	2.1	3.00	3.0	8.3
	0.02	11.2	2.3	2.73	3.3	9.9
	0.2	11.4	2.3	2.85	6.5	15.4
	2.0	10.3	2.2	2.96	22.0	117.4
Zn	0	6.4	1.9	2.20	8.4	29.9
	0.02	7.2	2.0	2.54	9.3	33.0
	0.2	10.7	2.2	2.65	20.2	44.0
	2.0	13.0	2.3	2.85	96.7	171.6
Mn	0	10.3	2.0	2.77	7.4	11.0
	0.05	11.8	2.3	2.82	16.5	12.1
	0.5	12.2	2.1	3.13	124.2	30.6
	5.0	12.3	2.2	2.88	742.8	170.2
Mo	0	11.1	2.2	3.08	0.43	0.55
	0.005	13.0	2.3	3.08	0.33	1.14
	0.05	11.8	2.1	3.07	0.37	6.65
	0.5	11.5	2.2	2.74	1.44	90.92
B	0	11.1	2.1	2.99	6.5	15.3
	0.02	11.1	2.0	3.07	7.8	14.9
	0.2	11.1	2.1	2.77	42.4	26.3
	2.0	10.9	2.0	2.86	252.8	53.6
Fe	0	12.0	2.1	2.57	27.1	42.3
	0.4	14.0	2.2	2.81	31.9	65.5
	4.0	10.3	2.1	2.47	80.8	170.2
	40.0	5.6	2.0	2.28	420.1	548.6

TABLE 11. Analysis of variance for seedling heights, measured on October 1987, showing linear and quadratic components of contrast tests separately for each macronutrient

Source		df	Douglas-fir		White spruce	
			SS	p*	SS	p*
Block		1	4.66	0.86	51.85	0.26
Nutrient		5	20017.26	0.00	11592.50	0.00
Level(nutrient)		18	39841.39	0.00	18027.80	0.00
N	Lin	1	12882.53	0.00	6232.86	0.00
	Quad	1	173.26	0.37	146.69	0.57
P	Lin	1	11002.38	0.00	4389.38	0.00
	Quad	1	3454.02	0.00	1096.73	0.13
K	Lin	1	7729.60	0.00	2257.58	0.03
	Quad	1	804.16	0.06	267.55	0.44
Ca	Lin	1	13.73	0.80	1.83	0.95
	Quad	1	4.16	0.89	0.08	0.99
Mg	Lin	1	38.37	0.67	117.58	0.61
	Quad	1	40.49	0.92	0.19	0.98
S	Lin	1	2313.70	0.00	1653.99	0.06
	Quad	1	1022.63	0.04	1525.84	0.07
Error mean square		23	8.8563		18.8919	

* p = probability for variance ratio "F".

TABLE 12. Analysis of variance for whole seedling dry weights, measured on October 1987, showing linear and quadratic components of contrast tests separately for each macronutrient

Source		df	Douglas-fir SS	Douglas-fir p*	White spruce SS	White spruce p*
Block		1	1.053	0.66	0.285	0.02
Nutrient		5	23.242	0.00	12.527	0.00
Level(nutrient)		18	51.654	0.00	20.920	0.00
N	Lin	1	14.023	0.00	6.404	0.04
	Quad	1	0.534	0.00	0.212	0.00
P	Lin	1	11.011	0.00	5.170	0.00
	Quad	1	3.914	0.00	1.273	0.00
K	Lin	1	11.322	0.00	3.388	0.00
	Quad	1	0.622	0.00	0.423	0.00
Ca	Lin	1	0.032	0.37	0.004	0.78
	Quad	1	0.011	0.60	0.030	0.43
Mg	Lin	1	0.000	0.95	0.088	0.18
	Quad	1	0.075	0.18	0.010	0.66
S	Lin	1	6.524	0.00	1.717	0.00
	Quad	1	1.732	0.00	1.480	0.00
Error mean square		23	0.0385		0.0467	

* p = probability for variance ratio "F".

TABLE 13. Analysis of variance for seedling heights, measured on October 1988, showing linear and quadratic components of contrast tests separately for each micronutrient

Source		df	Douglas-fir		White spruce	
			SS	p*	SS	p*
Block		1	2.18	0.88	50.41	0.73
Nutrient		5	1139.38	0.00	657.17	0.00
Level(nutrient)		18	9691.85	0.00	2850.89	0.00
Cu	Lin	1	1.32	0.67	0.04	0.92
	Quad	1	0.31	0.83	29.50	0.01
Zn	Lin	1	1899.11	0.00	1070.46	0.00
	Quad	1	52.31	0.01	21.46	0.02
Mn	Lin	1	0.47	0.80	82.43	0.00
	Quad	1	0.30	0.84	20.74	0.02
Mo	Lin	1	3.77	0.47	0.01	0.97
	Quad	1	209.08	0.00	47.63	0.00
B	Lin	1	869.45	0.00	0.50	0.70
	Quad	1	566.26	0.00	0.60	0.68
Fe	Lin	1	3464.03	0.00	1023.33	0.00
	Quad	1	2240.26	0.00	451.59	0.00
Error mean square		23	43.1471		29.4888	

* p = probability for variance ratio "F".

TABLE 14. Analysis of variance for whole seedling dry weights, measured on October 1988, showing linear and quadratic components of contrast tests separately for each micronutrient

Source		df	Douglas-fir		White spruce	
			SS	p*	SS	p*
Block		1	0.007	0.66	0.023	0.43
Nutrient		5	0.823	0.00	0.465	0.05
Level(nutrient)		18	7.448	0.00	2.570	0.00
Cu	Lin	1	0.005	0.71	0.002	0.71
	Quad	1	0.018	0.49	0.000	0.87
Zn	Lin	1	0.747	0.00	0.473	0.00
	Quad	1	0.004	0.75	0.000	0.92
Mn	Lin	1	0.000	0.98	0.012	0.42
	Quad	1	0.041	0.30	0.092	0.04
Mo	Lin	1	0.000	0.94	0.024	0.25
	Quad	1	0.309	0.01	0.055	0.19
B	Lin	1	0.636	0.00	0.034	0.17
	Quad	1	0.606	0.00	0.396	0.00
Fe	Lin	1	2.635	0.00	1.063	0.00
	Quad	1	2.049	0.00	1.440	0.00
Error mean square		23	0.0361		0.0169	

* p = probability for variance ratio "F".